PHYSIOLOGY AND REPRODUCTION

Potential Relationships Between Physical Traits and Male Broiler Breeder Fertility[1]

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ABSTRACT Genetic selection in primary broiler breeders may modify skeletal structure, possibly impeding semen transfer, and could alter the size and degree of fluctuating asymmetry (FA) of bilateral traits associated with fertility. Hence, we hypothesized specific morphometric traits could predict differential fertility. Sixty primary broiler breeder males from Strains A and B (n = 30/strain) were individually housed with an average of 10 females per male. Male fertility and sperm penetration (SP) through the perivitelline layer were estimated on fresh eggs. At 50 wk, BW, keel length (KL), posterior pelvic width and length (PPW, PPL), dorsal pelvic width and length (DPW, DPL), tarsometatarsal length and width (TL, TW), comb length and width (CL, CW), and wattle length, width, and area (WL, WW, WA) were measured. Results indicated that Strain A had smaller BW, KL, WL, WW, WA, CL, CW, PPL, DPL, and DPW. A higher degree of FA was found in Strain A TL and WL ($P < 0.05$), yet DPW FA was greater for Strain B ($P < 0.001$). In addition, DPW FA negatively correlated with Strain B fertility (r = –0.369; $P < 0.01$); however, other FA measurements did not correlate with estimated fertility or SP. Strain A WL correlated with SP (r = 0.383; $P < 0.01$) and fertility (r = 0.346; $P < 0.01$). Results indicate DPW alteration may impact semen transfer upon copulation, as Strain A fertility negatively correlated with DPW (r = –0.298; $P < 0.05$). This research provides evidence that morphometric traits might be useful to predict fertility in broiler breeders.

(*Key words*: broiler breeder, male fertility, skeletal conformation, fluctuating asymmetry)

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INTRODUCTION

The recent decline of fertility of naturally mated broiler breeder flocks (Reddy and Sajadi, 1990) is related, in part, to the differential reproduction among males, as some males have high fertility whereas others have low fertility (subfertile) and, hence, contribute to a reduction in overall flock fertility. Although male broiler breeder behavior (Burke and Mauldin, 1985; Jones and Mench, 1991) and physiology (Wishart and Palmer, 1986; Froman et al., 1992; Kirby et al., 1994) affect the level of fertility attained by individuals, male physical characteristics may also be important. The potential for physical traits to impact reproduction is evident when one considers the historical situation in the turkey industry. Subfertility in naturally mated toms reached a critical point at which reproduction could no longer be maintained without utilizing artificial insemination. Fertility problems were partially attributed to selection for increased BW (Kondra and Shoffner, 1955; Ogasawara et al., 1963) and modified breast size (Berg and Shoffner, 1954; Carte and Leighton, 1969), which reduced the physical ability of toms to mount and copulate successfully, hence inefficient semen transfer at the time of copulation likely contributed to the fertility decline in turkey breeders (Smyth and Leighton, 1953; Hale, 1955; Carte and Leighton, 1969). As with turkeys, broiler breeders have undergone intense selection pressure for production traits that consequently has altered birds' muscular distribution, breast size, and BW.

Genetic selection for traits such as growth rate and yield have been negatively associated with the expression of morphometric traits related to reproduction (Soller et al., 1965a; Siegel and Dunnington, 1985). Specifically, male BW is known to directly impact reproduction in broiler breeders (Wilson et al., 1979; Siegel and Dunnington, 1985). An additional consequence of selection for growth is that skeletal conformation and leg dimensions have likely been modified to physically support birds' bodies. These physical modifications may impede semen

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Abbreviation Key: CL = comb length; CW = comb width; DPL = dorsal pelvic length; DPW = dorsal pelvic width; FA = fluctuating asymmetry; KL = keel length; PPL = posterior pelvic length; PPW = posterior pelvic width; SP = sperm penetration; TL = tarsometatarsal length; TW = tarsometatarsal width; WA = wattle area; WL = wattle length; WW = wattle width.

transfer (Soller et al., 1965b; Wilson et al., 1979; Hocking and Duff, 1989; Siegel and Dunnington, 1985; Fontana et al., 1990), for example, through altered compatibility of the male and female cloacal positioning during copulation, which could reduce concomitant fertility.

Along with the potential for physical modifications to impact fertility, the degree of development of the secondary sexual characters could also affect the reproductive potential of an individual. For example, comb and wattle growth are androgen dependent (Dorfman, 1948; Zeller, 1971) and have been shown to correlate with a male's health status in red jungle fowl (Hamilton and Zuk, 1982). Sexual selection theory states that this differential expression (individual variation in the degree of phenotypic expression) of secondary sexual characters may reliably indicate individual male quality (Hamilton and Zuk, 1982; Kodric-Brown and Brown, 1984; Andersson, 1994). Evidence provided by Zuk et al. (1995) supports this theory, as when female red jungle fowl were given a choice of two males during a preference test, they more frequently mated with males possessing large combs.

Asymmetry refers to the random deviations from symmetry in the development of bilaterally symmetrical traits (i.e., primary wing feather length, tarsus length, and spur length) (Van Valen, 1962; Johnstone, 1994; Møller, 1994). Fluctuating asymmetry (FA), a specific type of asymmetry, occurs without any directionality, deviating in either direction with a normal distribution and a mean of zero (Møller, 1994). FA has been demonstrated to convey an individual's ability to cope with environmental and social stress (Leary and Allendorf, 1989; Parsons, 1990; Møller et al., 1995) and reflects male reproductive quality in some avian species, as poor quality males tend to be more asymmetric (Møller, 1990). In addition, females have been shown to prefer to mate with males that are more symmetric (Møller, 1992).

Because stress may negatively affect reproduction (Edens, 1983), environmental stressors such as extreme temperature (McDaniel et al., 1995) and feed restriction (Bartov et al., 1988; Sexton et al., 1989) could have a detrimental impact on fertility of male broiler breeders under commercial conditions. Hence, if stress reduces fertility and also increases FA, measuring the degree of FA may reliably identify males that are more likely to have low fertility.

The relationship between secondary sexual characters and fertility was previously confirmed in domestic fowl by McGary et al. (2002), who found that male broiler breeders with larger combs within specific strains were likely to have higher fertility, as a significant positive correlation was found between Strain A males and their individual fertility level. As such, if female broiler breeders more frequently crouch for and subsequently mate with males having large, symmetrical combs and wattles, differential fertility may be related to the fact that high-quality males secure a higher mating frequency, which should, in turn, improve reproduction. These previous findings led us to investigate wattle size, other relevant comb dimensions, and other morphological characteristics as sexual traits potentially indicating male fertility levels. The intent of this study was to characterize the relationship between male fertility and various physical traits in two male-selected strains (A and B) of primary broiler breeders. It has been previously demonstrated by McGary et al. (2002) that Strain A has lower mean fertility as well as reduced sperm penetration (SP) through the perivitelline layer of the ova. We predicted that males with lower fertility would have higher BW, altered pelvic and leg conformation, smaller secondary sexual characters, and a higher degree of FA in bilateral traits.

MATERIALS AND METHODS

Experimental Design

Two male-line genetic strains (A and B) of primary broiler breeders, used by the primary breeder company (undisclosed) for pure line regeneration, were investigated in this study. Both strains have undergone different genetic selection regimes. Strain A, in particular, was derived from a Cornish line with selection for breast yield and had greater fertility problems than Strain B, which has undergone selection for growth (McGary et al., 2002). Following commercial management practices for pure line selection, all birds were broilerized, defined as the provision of ad libitum feed to allow phenotypic expression of the broiler growth traits. Following broilerization, individuals were selected as pedigree birds at 7 wk of age. From 7 to 21 wk, males and females were reared in blackout housing on a feed-restriction program (undisclosed information).

At 21 wk, each male was randomly placed in an individual pedigree breeder pen containing an average of 10 females. Males were feed-restricted on a daily basis to maintain live weight (3,168 kcal/kg BW/d and 12% CP), whereas females were feed-restricted to maintain egg production. Each strain was maintained in an open-side house on a 16.5L:7.5D lighting program and managed according to standard operating procedures of the primary breeder facility.

A sample of 30 males within each genetic strain was randomly selected for this study. Following statistical consultation (E. Russek-Cohen, Department of Animal and Avian Sciences, University of Maryland, College Park, MD, personal communication), this sample size was considered sufficient to account for the high inter-individual variability reported in natural mating studies (Wishart et al., 1992). Data on fertility and SP through the perivitelline layer was collected for each experimental male at each of the following ages: period 1 (30 to 33 wk), period 2 (34 to 37 wk), period 3 (38 to 41 wk), period 4 (43 to 46 wk), and period 5 (48 to 51 wk). Comb and wattle dimensions were measured at early and late age periods, whereas leg and pelvic measurements were taken at age period 5. The experimental protocol was approved by the University of Maryland Animal Care and Use Committee.

Fertility and SP Through the Perivitelline Layer

Fertility was estimated by macroscopic assessment of the germinal disc (Bakst et al., 1997; Hazary et al., 2001) of four fresh-laid eggs collected from each experimental pen at each age period. During each farm visit at each age period, we took a random sample of four eggs per pen on a single afternoon to ensure that each egg represented a different female within each pen. Because the males were housed in individual pens, this allowed us to estimate percentage fertility for individual males. Eggs were stored at 13 C and 75% relative humidity and were evaluated within 5 d of collection. Estimated fertility (%) was calculated for individual males at each age period. It should be mentioned that McGary et al. (2002) demonstrated that this method of fertility estimation (based on the four-egg sample) strongly correlated with candling fertility, estimated from collections of all laid eggs during a full week for each age period.

Manual semen collection from naturally mating broiler breeders may be an inaccurate methodology to determine semen quality due to poor response to the collection procedure and because males regularly mate. Under these circumstances, SP rather than direct semen evaluation could more accurately assess semen transfer and the number of spermatozoa reaching the infundibulum upon ovulation (Wishart, 1987). After determining fertility of the sample eggs, the procedures outlined by Howarth and Donoghue (1997) were followed for quantitative determination of SP. Briefly, a 15- × 15-mm section of the perivitelline layer overlying the germinal disc was removed, washed 3× in PBS, and mounted on a Superfrost Plus slide.[3] After fixation (4% formalin), the perivitelline layer was stained with Schiff's reagent[4] to visualize sperm holes. Holes observed within a 5- × 5-mm eyepiece grid were counted at 40× and reported as mean SP per male (based on the four-egg sample) per age period.

Physical Measurements

Wattle length (WL), width (WW), area (WA), and comb length (CL) and width (CW) were measured for each male by PC image analysis[5] of digital pictures of the left and right sides of the head. Each picture includes a metric ruler for calibration. The computer mouse was used to trace WL, WW, WA, CL, and CW, and the distance (mm) or area (mm^2) was calculated by the Scion Image Analysis Software. The WL and CL were measured as the maximum horizontal distance between the front and the rear of the comb/wattle. The CW was measured as the maximum vertical distance from the highest peak of the comb to the base and WW as the maximum vertical distance from base of the wattle to the distal end. Tracing the perimeter of the wattle with the computer mouse allowed Scion software to calculate WA. The WW, WA, CL, and CW per male for the early and late age periods were determined. Because trait size did not differ between ages ($P > 0.05$), the mean trait size between these two measurements was calculated and used for subsequent statistical analyses.

At 50 wk (Strain A) and 48 wk (Strain B) of age, males were weighed and euthanized according to the breeder company's flock termination schedule. Digital calipers[6] were used to measure tarsometatarsal length (TL; from the tibio-tarsal joint to the joint of the hallux) and tarsometatarsal width (TW; the width of leg above the spur). A cloth measuring tape was used to measure keel length (KL), defined as the maximum distance from the anterior end of the sternum to the posterior end of the xyphoid process. The thoracic/pelvic regions were then skinned, and the majority of muscle mass was removed from the bones. After air-drying until the moisture content of the remaining muscle tissue was approximately 2 to 5%, the individually labeled carcasses were placed in a stainless steel tank (121.92 × 91.44 × 30.48 cm) that was covered with a plexiglass top containing screen-covered square openings measuring 21 × 25 cm for air circulation. Carcasses were placed on disposable cardboard trays on top of a layer of nonsterile cotton and covered with a second layer of cotton. Dermestid beetles (*Dermestes maculatus*) were added to the tank to engage in active tissue removal from the bones. The cleaned pelvises were carefully removed, placed in individual plastic bags, and frozen (–31 C) for 2 d to kill remaining adults, larvae, and eggs. Pelvises were rinsed in a mild detergent and allowed to air dry.

Posterior and dorsal pelvic dimensions were measured with digital calipers from the outermost processes located on the skeleton. The digital photos of the posterior (Figure 1a) and dorsal (Figure 1b) skeletal views include letters to denote the points at which the measurements were taken. Mean posterior pelvic length (PPL; Figure 1a) was calculated as (EA + FB)/2, and mean posterior pelvic width (PPW; Figure 1a) was calculated as (EF + CD + AB)/3. The PPW estimate was based on the average of measurements at three separate points, as this pelvic area varied greatly depending on where the measurement was taken. Mean dorsal pelvic length (DPL; Figure 1b) was calculated as (GI + HJ)/2, and mean dorsal pelvic width (DPW; Figure 1b) was (GH + IJ)/2. The degree of relative FA between the left (L) and right (R) bilateral traits (TL, TW, WL, WW, DPL, DPW, PPL, PPW) was calculated using the formula $|L-R|/(L+R)$ (Møller, 1995). Relative FA takes mean trait size into consideration in the calculation of FA (Møller, 1995; 1999). In addition, overall pelvic asymmetry was calculated as the mean FA in DPL, DPW, PPL, and PPW, whereas total FA was determined by calculating mean FA based on the degree of FA determined for all of the bilateral traits measured in this study.

Statistical Analyses

Univariate procedures were applied to determine normality and homogeneity of the residual variance in the

[3]Fisher Scientific, Pittsburgh, PA.
[4]Sigma Chemical Co., St. Louis, MO.
[5]Scion Corporation, Frederick, MD.
[6]Mitutoyo Corporation, Kawasaki, Kangawa, Japan.

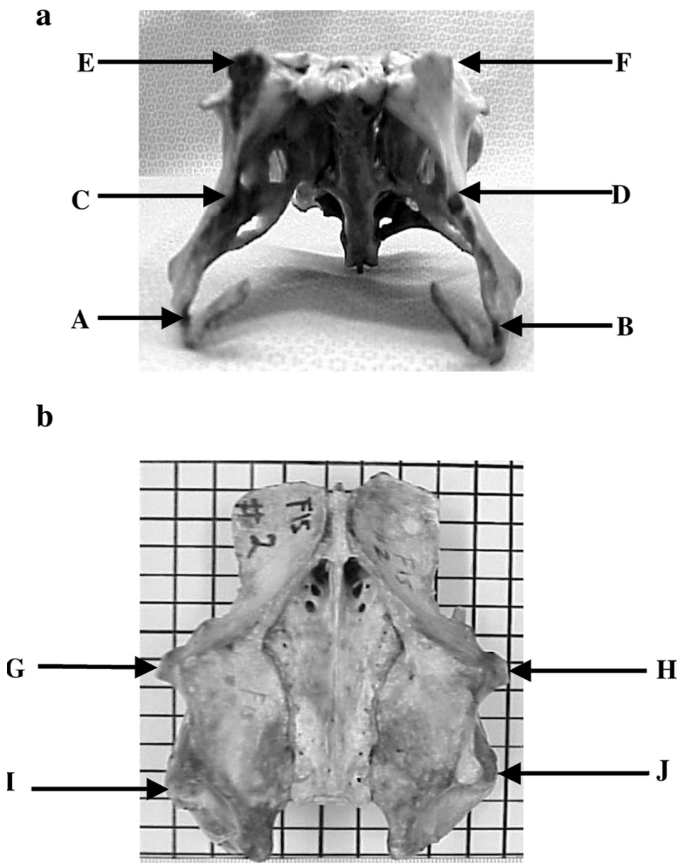

FIGURE 1. Digital photographs of the a) posterior and b) dorsal views of the thoraco-pelvic region of the male. Length and width measurements were taken using digital calipers at the outermost points of the processes, as denoted by the capital letters on each photograph. The posterior pelvic length (PPL) was calculated as (EA + FB)/2, posterior pelvic width (PPW) was (EF + CD + AB)/3. Dorsal pelvic length (DPL) was calculated as (GI + HJ)/2, and dorsal pelvic width (DPW) was (GH + IJ)/2.

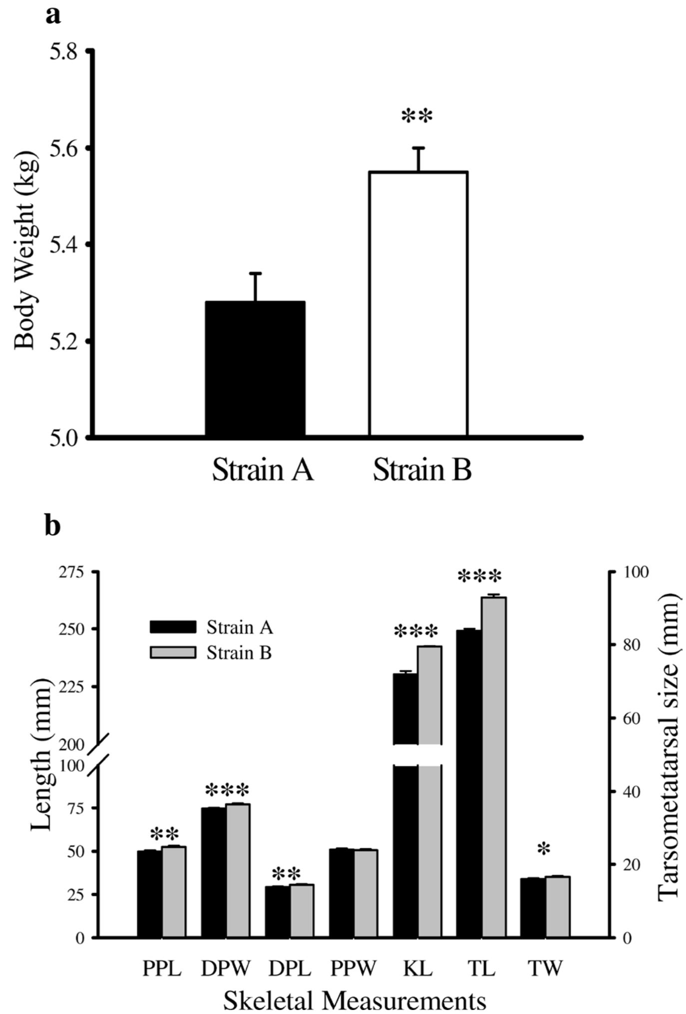

FIGURE 2. Differences between Strains A and B (mean ± SE) for a) BW and b) posterior pelvic length (PPL), dorsal pelvic width (DPW), dorsal pelvic length (DPL), posterior pelvic width (PPW), keel length (KL), tarsometatarsal length (TL), and tarsometatarsal width (TW). Statistical significance between each strain for each morphometric dimension has been denoted as *$P < 0.05$, **$P < 0.01$, or ***$P < 0.001$.

data. Physical strain differences were analyzed by the t-test. Data on fertility, SP values per male, were averaged across age to be used for the correlation analyses. Although the morphometric traits met the ANOVA assumptions, we used Kendall non-parametric correlation analysis for each strain to determine the potential relationships between fertility, SP, and the physical parameters as the fertility and SP data were not normally distributed. One outlier was removed from the Strain A correlation analysis between WL and SP and fertility. This male with very low fertility and SP had WL greater than two standard deviations from the mean. Although these correlations between WL and the fertility estimates were significant when this value was included, this individual's WL appeared to be driving the regression line; therefore, removal of this individual resulted in a stronger r-value. Data were analyzed using the SAS statistical package.[7] Significance for all statistical analyses was accepted at $P < 0.05$.

[7]SAS Institute, Inc., 1999. Version 8.2 ed. Cary, NC.

RESULTS

Strain A had lower BW ($P < 0.01$; Figure 2a), as well as specific conformational differences (Figure 2b, Y_1 axis) as compared to Strain B, including smaller PPL ($P < 0.01$), DPW ($P < 0.001$), DPL ($P < 0.01$), and KL ($P < 0.001$). Strain A leg dimensions (Figure 2b, Y_2 axis) followed a similar pattern of size reduction for TL ($P < 0.0001$) and TW ($P < 0.05$). The Kendall correlation analysis between the fertility estimates and all of the above physical traits within strain indicated a negative correlation between Strain A DPW and fertility, ($r = -0.298$; $P < 0.05$; Figure 3a) but not with SP ($P > 0.05$). This relationship between DPW and the fertility estimates was not significant for Strain B males ($P > 0.05$; Figure 3b). No additional correlations were found between BW, KL, DPL, PPL, PPW, TL, or TW and fertility estimates within either genetic strain ($P > 0.05$).

The sizes of the secondary sexual characters (WL, WW, WA, CL, CW) were smaller for Strain A as compared to

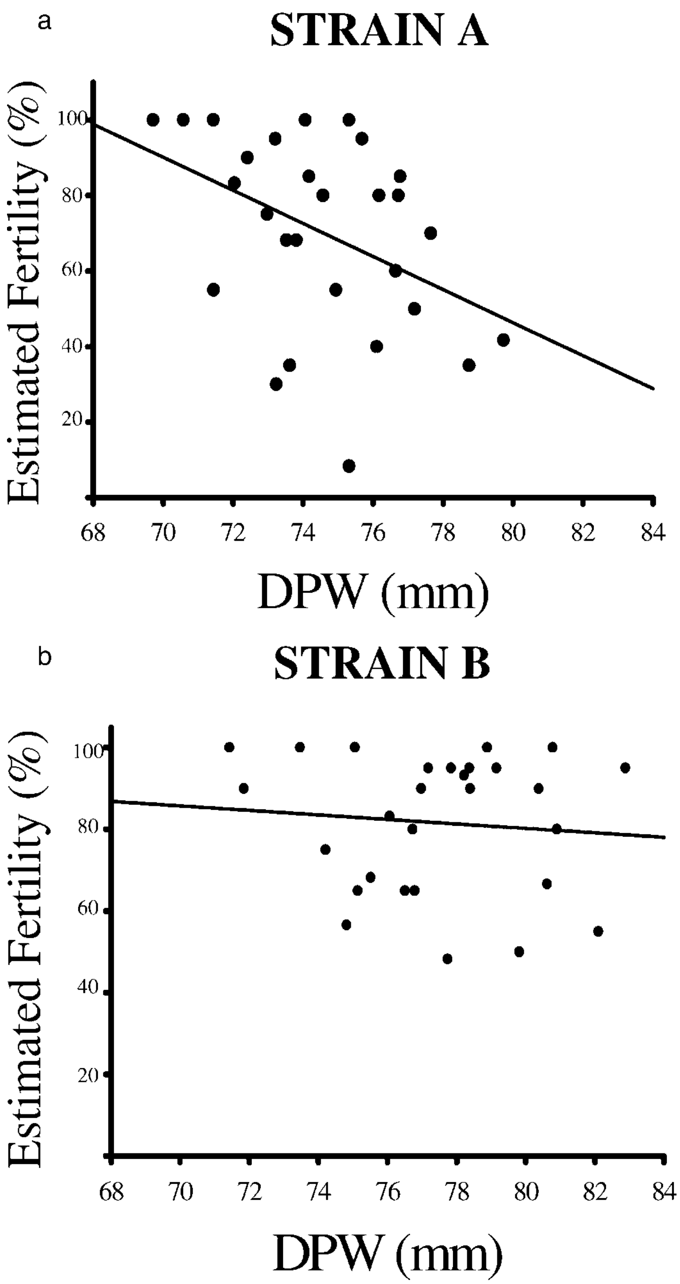

FIGURE 3. Correlations within Strains A and B between dorsal pelvic width (DPW) and fertility (Strain A, r = –0.298, $P < 0.05$; Strain B, $P > 0.05$).

Strain B ($P < 0.001$; Figure 4). Further analysis of these characters revealed that within Strain A, males with greater WL tended to have higher fertility (r = 0.346; $P < 0.01$; Figure 5a) and SP (r = 0.383; $P < 0.01$; Figure 5b). The same relationship was found for CW as well, which correlated with Strain A fertility (r = 0.296; $P < 0.05$; Figure 6a) and SP (r = 0.030; $P < 0.05$; 6b). However, no correlations were found between wattle dimensions and fertility estimates within Strain B.

Despite the smaller size of Strain A birds and their secondary sexual characters, the degree of FA (Figure 7) for TL ($P < 0.01$) and WL ($P < 0.05$) was greater than for Strain B. Conversely, FA of DPW was greater for Strain B ($P < 0.001$). Interestingly, this was the only FA measurement that negatively correlated with fertility (r = –0.3694, $P < 0.01$; Figure 8). The additional FA measurements (pelvic, wattle, and leg) did not show any correlations with fertility or SP within either strain ($P > 0.05$). In addition, we calculated mean pelvic FA and overall FA per male with the expectation that these values would provide a better overall measure of FA. However, total FA (Strain A = 0.038 ± 0.004; Strain B = 0.040 ± 0.003) and pelvic FA (0.023 ± 0.002, 0.028 ± 0.011) were not different between Strains A and B, respectively ($P > 0.05$), nor did these measures of FA correlate with fertility or SP ($P > 0.05$).

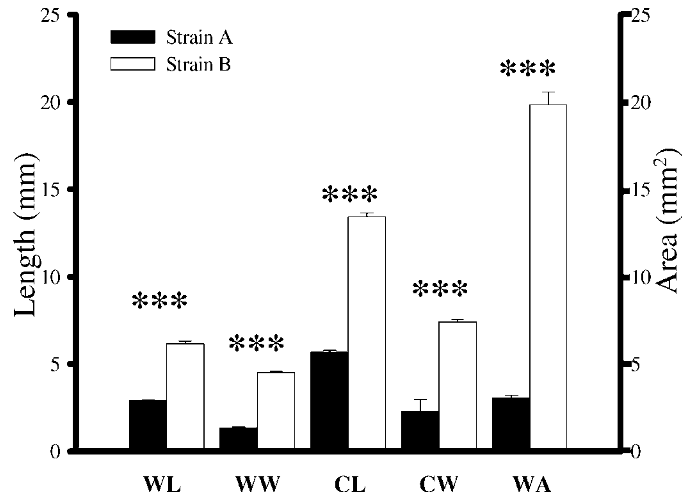

FIGURE 4. Differences (mean ± SE) between Strains A and B for wattle length (WL), wattle width (WW), comb length (CL), comb width (CW) (as indicated by the Y_1 axis in mm), and wattle area (WA) (as indicated by the Y_2 axis, mm^2). Statistical significance between each strain for each morphometric dimension has been denoted as ***$P < 0.001$.

DISCUSSION

The goal of the current experiment was to characterize the relationships between physical traits and fertility levels within two genetically divergent strains of primary broiler breeders. Surprisingly our findings showed Strain A males to have lower BW. This finding was contrary to our prediction that smaller males would have higher fertility due to better mating ability, which was based on previous works showing a tendency for reproductive fitness to decline as selection pressure for BW increases (Siegel and Dunnington, 1985). Furthermore, because BW did not correlate with fertility or SP in either of the strains we investigated, it seems unlikely that BW in itself directly impacted male mating ability at least in these genetic strains. Although little empirical evidence is available regarding the relationship between BW and fertility in broiler breeders, earlier studies have demonstrated a negative relationship between BW and fertility in naturally mated turkeys (Berg and Shoffner, 1954; Kondra and Shoffner, 1955). However, our findings are in agreement with Carte and Leighton (1969), who found no effect of BW on turkey fertility. Consequently, our finding suggests that rather than BW per se, other factors

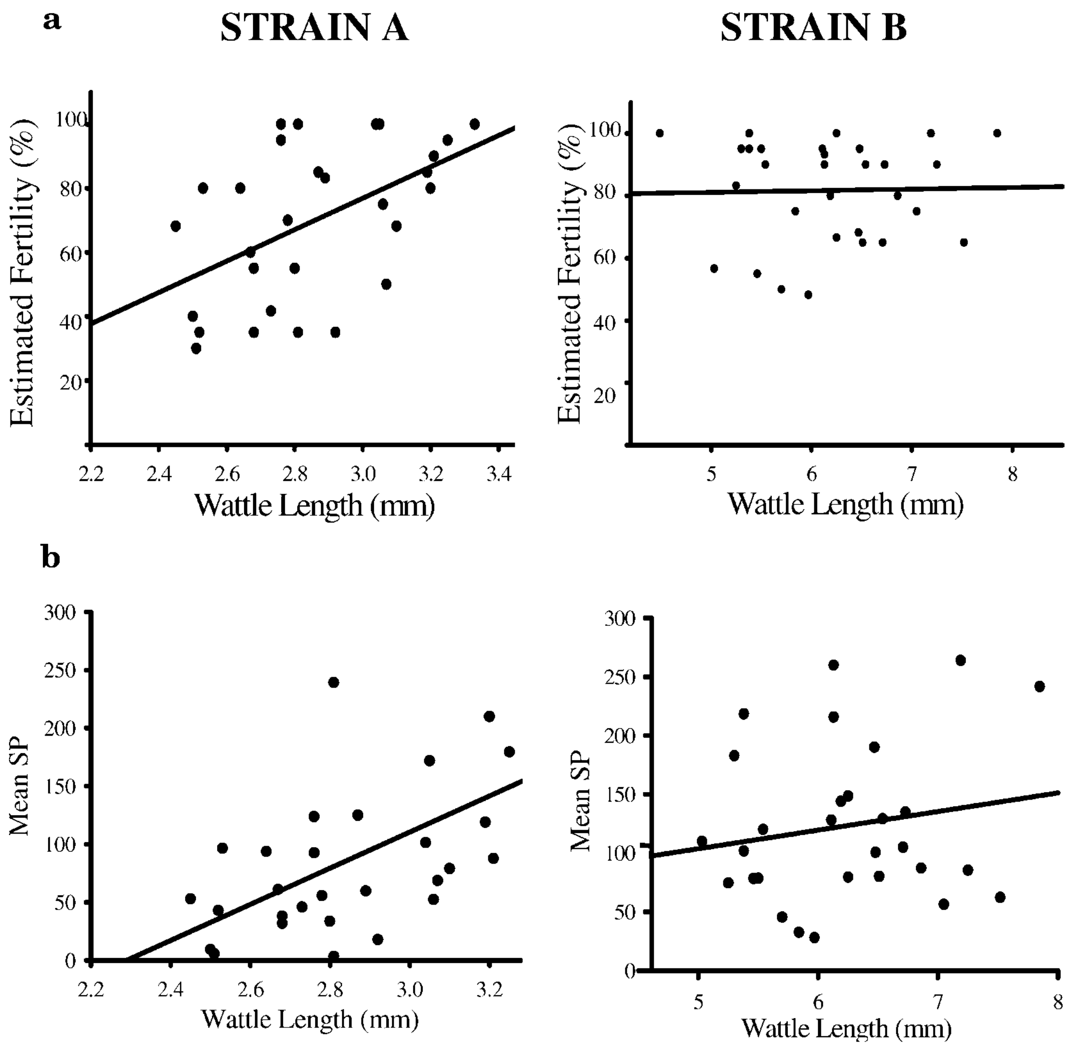

FIGURE 5. Correlations within Strains A and B between a) wattle length and fertility (Strain A, r = 0.254, $P < 0.05$; Strain B, $P > 0.05$); and b) wattle length and sperm penetration (SP) (Strain A, r = 0.383, $P < 0.01$; Strain B, $P > 0.05$).

such as specific musculo-skeletal characteristics (Carte and Leighton, 1969) may have impacted a male's ability to copulate successfully. Hence, the next logical step in our experiment was to determine if fertility levels were related to KL, pelvic conformation, or leg dimensions.

The intent of this experiment was to evaluate fertility under natural mating (commercial) conditions. Because manual semen collections may have biased the results of the original purpose of the study, and because the different mating activities of our experimental males would have caused an uncontrollable effect on the quality of the ejaculate collected, we decided against evaluation of semen quality in this study. Nevertheless, we recognize the importance of semen quality and its effects on differential male fertility as demonstrated by different authors previously (Froman and Bernier, 1987; Froman et al., 1992). Contrary to our prediction that larger musculo-skeletal dimensions (Wilson et al., 1979; Duncan et al., 1990) would impede semen transfer and reduce fertility, we found, in accordance with their smaller BW, that the Strain A males had smaller KL, DPW, DPL, and PPL as compared to Strain B. Nonetheless, pelvic conformation may be a useful parameter to predict fertility within Strain A, as we found fertility significantly declined as DPW increased. It is important to note that since Strain A has undergone intense selection for yield, it is likely that the skeletal structure was simultaneously modified in order to accommodate increased breast conformation. Therefore, it is possible that the widening of the DPW might have interfered with successful semen transfer for some males (e.g., by increased distance between the male and female cloaca upon copulation). In addition, it was suggested by McGary et al. (2001) that fertility problems in broiler breeders are unlikely related to a lack of courtship or to reduced mating frequency. Hence, the potential impact of genetic selection for growth on fertility seems to be more closely related to specific aspects of musculo-skeletal structure for any given poultry strain, such as DPW in the case of Strain A.

We anticipated variation in leg dimensions to impact mating and semen transfer ability in much the same manner as pelvic structure, particularly if the genetic selection resulted in males with altered leg size. In accordance with the potential for musculo-skeletal modifications to

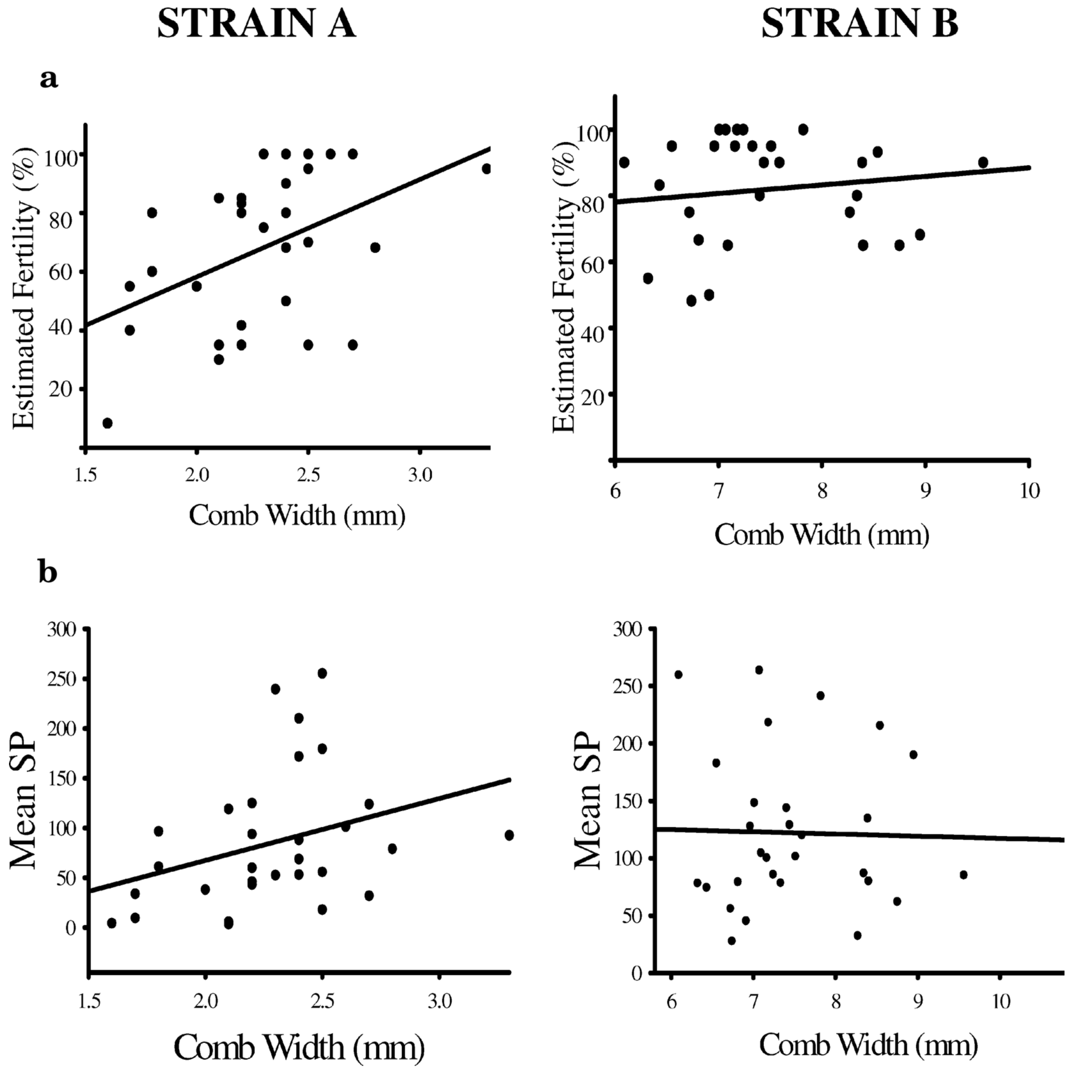

FIGURE 6. Correlations within Strains A and B between a) comb width and fertility (Strain A, r = 0.298, $P < 0.05$; Strain B, $P > 0.05$); and b) comb width and sperm penetration (SP) (Strain A, r = 0.3011, $P < 0.05$; Strain B, $P > 0.05$).

impede semen transfer, variability in leg size could, for example, alter the intersexual cloacal distance upon mating. Although TL and TW were significantly smaller for Strain A, the strain with poorer fertility, neither TL nor TW correlated with fertility or SP within either strain. These results suggest, therefore, that leg size does not seem to have a direct impact (positive or negative) on male fertility levels.

In addition to skeletal dimensions, we investigated comb and wattle size as potential phenotypic fertility correlates. Our results showed that Strain A males had smaller WL, WW, WA, CL, and CW than Strain B. Moreover, WL and CW positively correlated with fertility and SP in Strain A, providing further evidence of the relationships between differential phenotypic expression of secondary sexual traits and an individual's reproductive success, in agreement with the results reported by McGary et al. (2002) for comb area. However, our results provided no evidence in support of the measurements of these sexual traits as fertility correlates for Strain B. These findings therefore reinforce the potential use of secondary sexual characters as reliable fertility indicators within at least some genetic strains of broiler breeders.

Broiler breeders may face several nonspecific stressors, such as heat stress, feed restriction, management, and social stress that may have altered the degree of FA of bilateral traits as indicated previously. In support of our prediction that differential FA among males could be used as a tool to reliably select males of high reproductive quality (Møller, 1990), our results showed that although Strain A males had shorter TL and WL as compared to Strain B, they had a higher degree of FA for these measurements. Hence, it is possible that overall, males within Strain A were more prone to stress, which would result in a higher degree of FA, as stressors have been shown to influence the degree of FA in wild birds (Parsons, 1990) and in the domestic fowl (Møller et al., 1995).

Although we did not present data on the physiological stress response, serum samples from these males were analyzed for corticosterone, and those data have been submitted for publication elsewhere (S. McGary et al., unpublished data). In addition to environmental stres-

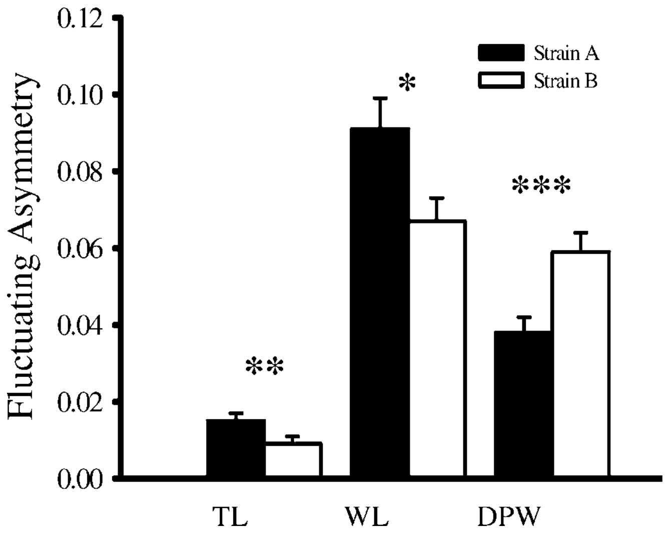

FIGURE 7. Mean ± SE of the degree of fluctuating asymmetry (FA) between the left and right tarsometatarsal length (TL), wattle length (WL), and dorsal pelvic width (DPW) for Strains A and B, respectively. Statistical significance between each strain for each morphometric dimension has been denoted as $^*P < 0.05$, $^{**}P < 0.01$, or $^{***}P < 0.001$).

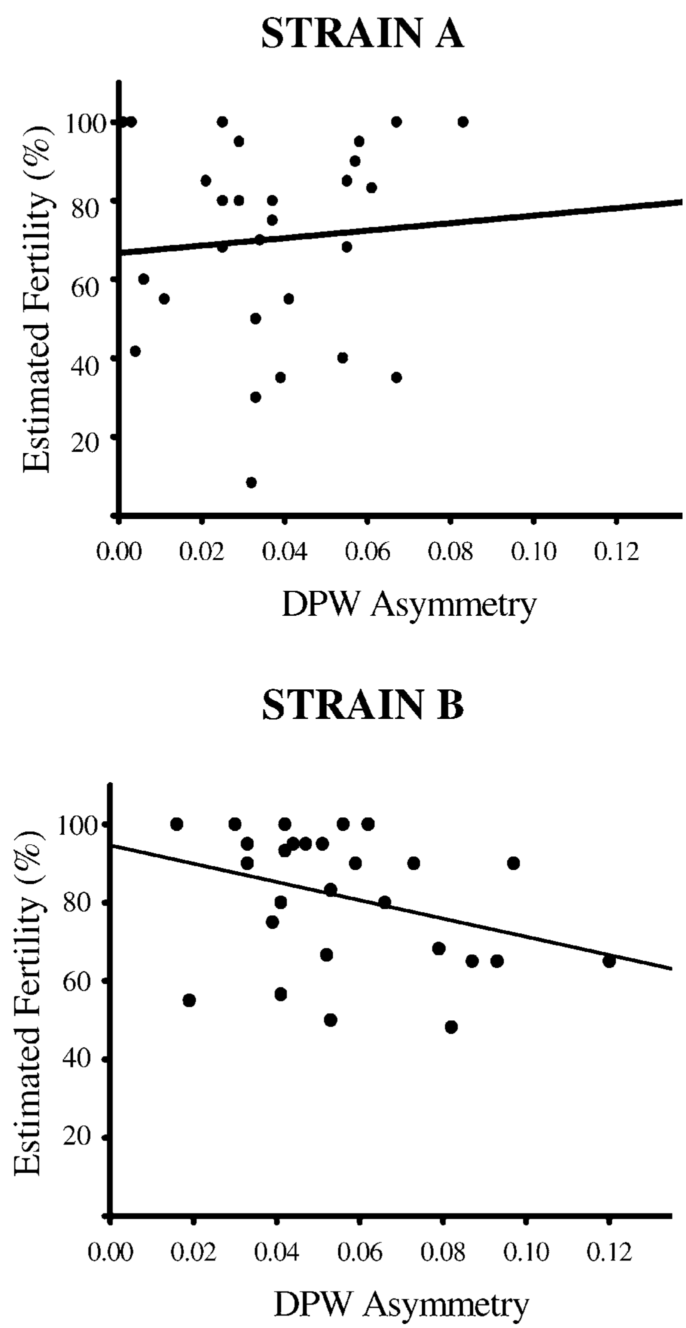

FIGURE 8. Correlations (within Strains A and B) between the degree of fluctuating asymmetry of dorsal pelvic width (DPW) and fertility for Strains A ($P > 0.05$) and B ($r = -0.369$, $P < 0.01$), respectively.

sors, the degree of energetic investment in growth reflects the symmetry of traits such as the tarsi (Swaddle and Witter, 1994; Rintamaki et al., 1997). Consequently, it is possible that the high-energy investment into growth might have constrained the ability of Strain A males to invest in development of highly symmetrical bilateral traits (Møller et al., 1995). However, contrary to our predictions, we did not find further relationships between the degree of FA of secondary sexual traits and fertility or SP within the genetic strains investigated in this study, despite the abundant existing literature that has demonstrated an inverse relationship between FA of secondary sexual characters and reproductive success in wild species (Møller, 1990; Morris and Casey, 1998; Cadėe, 2000).

Similar to the potential relationships with the development of secondary sexual characters, we also predicted FA in the musculo-skeletal measurements to negatively correlate with male fertility. This was partially supported by the finding that Strain B males with a greater degree of FA of DPW had lower fertility. As a more in-depth exploration of the impact of FA on fertility, we also estimated overall pelvic FA and total FA as fertility correlates, because we expected these comprehensive estimates of FA could better indicate male quality (Møller et al., 1995). However, neither of these FA estimates correlated with fertility or SP in either strain. Therefore, at least in this work, overall FA does not seem to characterize a male's fertility potential.

In conclusion, the present study provides further evidence suggesting the potential for musculo-skeletal traits, specifically DPW, and secondary sexual characters, namely CL and WL, to indicate male fertility levels in some genetic strains of primary broiler breeders. For example, Strain A DPW correlated with fertility levels, suggesting a direct impact of pelvic conformation on male's physical ability to mount and successfully inseminate upon cloacal contact. In addition, the positive correlation between WL, CL, and fertility in Strain A indicates that the development of secondary sexual characters may convey male reproductive quality in some genetic strains. Despite the fact that our results did not strongly support the use of FA to predict fertility potential, we suggest that the relationship between FA and fertility in broiler breeder males should be further explored, as Strain A, which had lower fertility, also had a higher degree of FA in TL and WL. Furthermore, the degree of FA of DPW in Strain B offers some potential as a fertility indicator in this strain that should be further investigated, although in general this strain was characterized by the lack of correlation between fertility and SP with any of the phenotypic traits investigated in this study. Because of the discrepancy of results between these two genetic strains, we suggest that independent strain evaluation must be conducted to characterize the most reliable phenotypic fertility indicators in each case.

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REFERENCES

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, NJ.

Bakst, M. R., S. K. Gupta, and V. Akuffo. 1997. Comparative development of the turkey and chicken embryo from cleavage through hypoblast formation. Poult. Sci. 76:83–90.

Bartov I., S. Bornstein, Y. Lev, M. Pines, and J. Rosenberg. 1988. Feed restriction in broiler breeder pullets: Skip-a-day versus skip-two-days. Poult. Sci. 67:809–813.

Berg, R. W., and R. N. Shoffner. 1954. The relationship between 24-week body measurements and reproductive performance. Poult. Sci. 33:1043.

Burke, W. H., and J. H. Mauldin. 1985. Reproductive characteristics of broiler breeder males from flocks with low fertility. Poult. Sci. 64:73. (Abstr.)

Cadėe, N. 2000. Parent barn swallow fluctuating asymmetry and offspring quality. J. Avian Biol. 31:495–503.

Carte, I. F., and A. T. Leighton. 1969. Mating behavior and fertility in the large white turkey. Poult. Sci. 48:104–114.

Dorfman, R. I. 1948. The relative reactivity of the comb of various breeds of chicks to androgens. Studies on the bioassay of hormones. Endocrinology 42:7–14.

Duncan, I. J. H., P. M. Hocking, and E. Seawright. 1990. Sexual behaviour and fertility in broiler breeder domestic fowl. Appl. Anim. Behav. Sci. 26:201–213.

Edens, F. W. 1983. Effect of environmental stressors on male reproduction. Poult. Sci. 62:1676–1689.

Fontana, E. A., W. D. Weaver, and H. P. Van Krey. 1990. Effects of various feeding regimens on reproduction in broiler breeder males. Poult. Sci. 69:209–216.

Froman, D. P., and P. E. Bernier. 1987. Identification of heritable spermatozoal degeneration within the ductus deferens of the chicken (*Gallus domesticus*). Biol. Reprod. 37:969–977.

Froman, D. P., J. D. Kirby, and A. M. Al-Aghbari, 1992. Analysis of the combined effect of the spermatozoal degeneration allele (*Sd*) and homozygosity of the rose comb allele (*R*) on the duration of fertility of roosters (*Gallus domesticus*). Poult. Sci. 71:1939–1942.

Hale, E. B. 1955. Defects in sexual behavior as factors affecting fertility in turkeys. Poult. Sci. 34:1059–1067.

Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218:384–387.

Hazary, R. C., H. J. Staines, and G. J. Wishart. 2001. Assessing the effect of mating ratio on broiler breeder performance by quantifying sperm: egg interaction. J. Appl. Poult. Res. 10:1–4.

Hocking, P. M., and S. R. I. Duff. 1989. Musculo-skeletal lesions in adult male broiler breeder fowls and their relationships with body weight and fertility at 60 weeks of age. Br. Poult. Sci. 30:777–784.

Howarth, B. Jr., and A. M. Donoghue. 1997. Predicting fertility. IV. Determination of holes made by sperm in the perivitelline layer of laid eggs. Pages 93–97 in Techniques for Semen Evaluation, Semen Storage, and Fertility Determination. M. R. Bakst and H. C. Cecil, ed. Poultry Science Association, Savoy, IL.

Johnstone, R. A. 1994. Female preference for symmetrical males as a by-product of selection for mate recognition. Nature 372:172–174.

Jones, M. E., and J. A. Mench. 1991. Behavioral correlates of male mating success in a multisire flock as determined by DNA fingerprinting. Poult. Sci. 70:1493–1498.

Kirby, J. D., H. N. Engel, Jr., and D. P. Froman. 1994. Analysis of subfertility associated with homozygosity of the rose comb allele in the male domestic fowl. Poult. Sci. 73:871–878.

Kodric-Brown, A., and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. Am. Nat. 124:303–323.

Kondra, P. A., and R. N. Shoffner. 1955. Heritability of some body measurements and reproductive characters in turkeys. Poult. Sci. 34:1262–1267.

Leary, R. L., and F. W Allendorf. 1989. Fluctuating asymmetry as an indicator of stress: Implications for conservation biology. Trends Ecol. Evol. 4:214–217.

McDaniel, C. D., R. K. Bramwell, J. L. Wilson, and B. Howarth, Jr. 1995. Fertility of male and female broiler breeders following exposure to elevated ambient temperatures. Poult. Sci. 74:1029–1038.

McGary, S., I. Estevez, M. R. Bakst, and D. L. Pollock. 2002. Phenotypic traits as reliable indicators of fertility in male broiler breeders. Poult. Sci. 81:102–111.

McGary, S., I. Estevez, and E. Russek-Cohen, 2001. Can differential fertility of male broiler breeders be explained by differences in reproductive and aggressive behaviour? Page 83 in Proceedings of the 35th International Congress of the International Society of Applied Ethology. J. P. Garner, J. A. Mench, and S. P. Heekin, ed. The Center for Animal Welfare at UC Davis, Davis, CA.

Møller, A. P. 1990. Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. Anim. Behav. 40:1185–1187.

Møller, A. P. 1992. Female swallow preference for symmetrical male sexual ornaments. Nature 357:238–240.

Møller, A. P. 1994. Directional selection on directional asymmetry: Testes size and secondary sexual characters in birds. Proc. R. Soc. Lond. Ser. B 258:147–151.

Møller, A. P., G. S. Sanotra, and K. S. Vestergaard. 1995. Developmental stability in relation to population density and breed of chickens *Gallus gallus*. Poult. Sci. 74:1761–1771.

Møller, A. P., G. S. Sanotra, and K. S. Vestergaard. 1999. Developmental instability and light regime in chickens (*Gallus gallus*). Appl. Anim. Behav. Sci. 62:57–71.

Morris, M. R., and K. Casey. 1998. Female swordtail fish prefer symmetrical sexual signal. Anim. Behav. 55:33–39.

Ogasawara, F. X., H. Abplanalp, and V. S. Asmundson. 1963. The effect of selection for body weight on reproduction in turkey hens. Poult. Sci. 42:838–842.

Parsons, P. A. 1990. Fluctuating asymmetry: an epigenetic measure of stress. Biol. Rev. Camb. Philos. Soc. 65:131–145.

Reddy, R. P. K., and A. Sajadi. 1990. Selection for growth and semen traits in the poultry industry: what can we expect in the future? Pages 47–59 in Control of Fertility in Domestic Birds. J. P. Brillliard, ed. INRA, Paris.

Rintamaki, P. T., R. V. Alatalo, J. Hoglund, and A. Lundberg. 1997. Fluctuating asymmetry and copulation success in lekking black grouse. Anim. Behav. 54:265–269.

Sexton, K. J., J. A. Renden, D. N. Marple, and R. J. Kempainen. 1989. Effects of dietary energy on semen production, fertility, plasma testosterone, and carcass composition of broiler breeder males in cages. Poult. Sci. 68:1688–1694.

Siegel, P. B., and E. A. Dunnington. 1985. Reproductive complications associated with selection for broiler growth. Pages 55–72 in Poultry Genetics and Breeding. W. G. Hill, J. M. Manson, and D. Hewitt, ed. British Poultry Science Ltd., Longman Group, Harlow, England.

Smyth, J. R., Jr., and A. T. Leighton, Jr. 1953. A study of certain factors affecting fertility in the turkey. Poult. Sci 18:236–243.

Soller, M., H. Schindler, and S. Bornstein. 1965b. Semen characteristics, failure of insemination and fertility in Cornish and White Rock males. Poult. Sci. 44:424–432.

Soller, M., N. Snapir, and H. Schlinder. 1965a. Heritability of semen quantity, concentration and motility in White Rock roosters, and their genetic correlation with rate of gain. Poult. Sci. 44:1527–1529.

Swaddle, J. P., and M. S. Witter. 1994. Food, feathers, and fluctuating asymmetries. Proc. R. Soc. Lond. Ser. B 255:147–152.

Van Valen, L. 1962. A study of fluctuating asymmetry. Evolution 16:125–142.

Wilson, H. R., N. P. Piesco, E. R. Miller, and W. G. Nesbeth. 1979. Prediction of the fertility potential of broiler breeder males. World's Poult. Sci. J. 35:95–118.

Wishart, G. J. 1987. Regulation of the length of the fertile period in the domestic fowl by numbers of oviducal spermatozoa. J. Reprod. Fertil. 80:493–498.

Wishart, G. J., and F. H. Palmer. 1986. Correlation of the fertilising ability of semen from individual male fowls with sperm motility and ATP content. Br. Poult. Sci. 27:97–102.

Wishart, G. J., H. J. Staines, and M. G. Steele. 1992. A method for predicting infertility in naturally-mated chickens and demonstration of gross variation in sperm transfer efficiency. Pages 631–634 in Proceedings of the 19th World's Poultry Congress. Volume 1. World's Poultry Science Association, Amsterdam.

Zeller, F. J. 1971. The effect of testosterone and dihydrotestosterone in the comb, testes, and pituitary gland of the male fowl. J. Reprod. Fertil. 25:125–127.

Zuk, M., S. L. Pompa, and T. S. Johnsen. 1995. Courtship displays, ornaments, and female mate choice in captive red jungle fowl. Behaviour 132:821–836.